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ORIGINAL PAPER

Marker-based introduction of three quantitative-trait loci conferring resistance to *Fusarium* head blight into an independent elite winter wheat breeding population

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Abstract *Fusarium* head blight (FHB) is one of the most important wheat diseases that causes yield and quality losses as well as contamination with deoxynivalenol (DON). This study aimed for marker-based introduction of three previously mapped QTLs from two German winter wheat resistance sources into an elite background unrelated to the mapping population. A double cross (DC) served as initial population that combined two resistance donor-QTL alleles from "Dream" (*Qfhs.lfl-6AL, Qfhs.lfl-7BS*) and one donor-QTL allele from "G16-92" on chromosome 2BL with two high yielding, susceptible elite winter wheats ("Brando", "LP235.1"). The initial population of 600 DC-derived F_1 lines was selected with SSR markers for the respective QTLs. After two marker-selection steps, each of eight marker classes was represented by 9–22 lines possessing the respective donor-QTL allele or all possible combinations thereof in the homozygous state. The effect of the QTLs was estimated by field tests at four locations inoculated with *Fusarium culmorum*. Resistance was measured as the mean of multiple FHB ratings (0–100%). Marker classes incorporating only one QTL were not significantly more resistant than the class without any QTL, the combination of two donor-QTL alleles reduced FHB significantly. On average, lines with *Qfhs.lfl-6AL* were significantly taller than lines without this QTL. A considerable variation for FHB resistance was found in all marker classes. Marker-based introduction of two QTLs enhanced mean FHB rating by about 40 percentage points, the selected plants, however, were, on average, significantly taller. Both findings strongly support a phenotypic selection following after marker-based introduction of effective QTLs.

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Introduction

Fusarium head blight (FHB) is one of the most common wheat (*Triticum aestivum* L.) diseases worldwide leading to yield reduction and poor grain quality. Resistance breeding is a promising tool to reduce FHB in wheat. Resistance to FHB is quantitatively inherited with a continuous distribution among the progeny (Bai and Shaner 1994). In European winter wheat germplasm several populations have been mapped for FHB resistance: "Renan" (Gervais et al. 2003), "Arina" (Paillard et al. 2004; Semagn et al. 2007), "Fundulea 201-R" (Shen et al. 2003), "Cansas" (Klahr et al. 2004), "G16-92" (Schmolke et al. 2008), and "Dream" (Schmolke et al. 2005). Two to nine QTL were detected per population individually explaining 2–22% of the phenotypic variance. Compared to "Sumai 3" and its derivatives, these effects are smaller and many of the beneficial QTL alleles were not stable across environments. Two of these QTLs have been recently validated in a backcross population (Haeberle et al. 2007), however, this study used the

same genetic background than the previous mapping study (Schmolke et al. 2005). For their use in practical plant breeding it is, however, crucial to estimate the effects of the mapped QTLs in an independent elite genetic background (Young 1999). This is necessary, because QTL positions as well as effects are not precisely estimated in individual mapping experiments due to sampling effects caused by using a restricted population size (Melchinger et al. 1998). The importance of QTL validation before applying marker-assisted selection is illustrated by the lack of QTL congruency across three mapping populations both using the Swiss winter wheat variety "Arina" as resistant parent (Paillard et al. 2004; Draeger et al. 2007; Semagn et al. 2007). The objective of the present study was the marker-based introduction of three previously mapped QTLs from the German winter wheats "Dream" and "G16-92" in an independent genetic background and testing their effects in several environments.

Materials and methods

Initial population development

Two mapping populations of 145 and 136 recombinant inbred lines (RILs) were developed from the winter wheat crosses Dream (resistant)/Lynx (susceptible) and G16-92 (resistant)/Hussar, respectively, in previous studies (Schmolke et al. 2005, 2008). "Dream" (Disponent/Kronjuwel//Monopol/3/Orestis) is a German elite winter wheat variety released in 1999, and the breeding line "G16-92" (H. Walther, German Federal Centre for Breeding Research on Cultivated Plants, Grünbach, Germany) descends from the Swiss cultivar Arina, Cariplus (Caribo/Ibis), Töring 5, and a Mexican landrace. Lynx (CWW-4442-64/Rendezvous) and Hussar (Squadron/Rendezvous) are British dwarf cultivars developed by Cambridge Plant Breeders (Cambridge, UK) and Syngenta (former: Imperial Chemical Industries), respectively. In the Dream/Lynx population, the SSR markers GWM 82 on chromosome 6AL (*Qfhs.lfl.6AL*) and GWM 46 on chromosome 7BS (*Qfhs.lfl.7BS*) explained 19.3 and 20.8% of the phenotypic variation for FHB resistance and the map distance from the peak of the respective QTL was 2 and 8 cM, respectively (Schmolke et al. 2005). In the G16-92/Hussar population, a major QTL was identified on chromosome 2BL near the marker GWM 47 that accounted for 17.8% of the phenotypic variation in a 2 cM distance to the peak of the QTL. All three QTL were stable across four environments. For simplicity, we refer to the chromosomal segment defined by the marker as QTL in the paper throughout. Donor-QTL alleles are numbered according to their chromosomal localization, e.g. donor-QTL 2BL.

The best RIL of each cross was selected by FHB rating in a previous generation after inoculation and served as donor parent in the present study so that some of the beneficial genes from the short, high-yielding parents of the mapping populations, "Lynx" and "Hussar", could be recovered. The presence of the target-QTL alleles in the RILs was verified using the mentioned molecular markers in advance. Because we wanted to combine the QTLs from two genetically different resistance sources in one step, the following double cross was performed in early 2001 in a greenhouse programme: P1/P2//P3/P4. For producing single crosses, resistant RILs (P1 and P3) of the mapping populations Dream/Lynx (P1) and G16-92/Hussar (P3), respectively, were crossed with Brando (P2) and LP235.1 (P4) in the greenhouse in early 2000. Brando is a high-yielding variety registered in Germany and LP235.1 a high-yielding breeding line from KWS LOCHOW GmbH. The double cross (DC) should result in equal frequencies of all donor-QTL alleles of 0.25. Six hundred randomly chosen DCF_1 individuals served as initial population for this study.

Marker selection

In 2001, the 600 DCF_1 seeds were planted in plastic trays. At the three-leaf stage, about 2 cm of leaf tissue was harvested separately from each seedling and frozen at −80°C for DNA isolation. All plant DNA was isolated from young leaves using the mini-prep CTAB method adapted from Saghai Maroof et al. (1984). Microsatellite designation, composition and primer sequences were reported by Röder et al. (1998) or have not yet been published. In general, a PCR protocol according to Röder et al. (1998) with 35 cycles instead 45 cycles of 1 min 94°C denaturation, 1 min 50°C (or 55 or 60°C depending on the primer) annealing and 1 min of 72°C extension followed using a final extension step of 5 min 72°C was used. For detection of PCR product on an ABI3700 or ABI3100 DNA sequencer running Genescan and Genotyper software, one of the primers from each pair was synthesized with the 5′end-nucleotide labeled with fam, hex or ned.

All 600 DCF_1 plants were screened for donor-QTL alleles located on chromosomes 2BL, 6AL and 7BS using the SSR markers GWM47, GWM82, and GWM46, respectively. These markers were selected because they were (1) the nearest available SSR markers to the respective QTL and (2) diagnostic for the alleles of the other parents (Table 1). Sixty DCF_1 plants possessing the donor-QTL alleles individually or jointly in the heterozygous state were marker selected, vernalized in a growth chamber, transplanted to the field nursery and selfed. Each DCF_1 plant was harvested separately at maturity. Sixty individual F_2 plants of each of the marker-selected 60 DCF_1 lines were planted in plastic trays, and leaf samples were collected for

Table 1 Allele sizes in base pairs (bp) of the three SSR markers GWM82, GWM46, and GWM 47 of the parents of the double crosses and the susceptible parents of the mapping populations. Allele size of the donor is printed in bold

SSR marker	Chromosome	Donor	Parents					
			G16-92 (bp)	Hussar (bp)	Dream (bp)	Lynx (bp)	Brando (bp)	LP235.1 (bp)
GWM82	6AL	Dream	145	145	**140**	145	145	145
GWM46	7BS	Dream	175	160	**158**	160	160	160
GWM47	2BL	G16–92	**160**	150	0[a]	150	150	150

[a] Occurrence of a null allele

SSR analyses as described above. A total of 3,600 plants were genotyped and those plants possessing either one of the three donor-QTL alleles individually or any of their combinations in the homozygous state were transplanted to the nursery for multiplication. Each plant was harvested separately resulting in $F_{2:3}$ lines. From each of the eight possible marker classes, 9–22 $F_{2:3}$ lines (in total 113) were tested for FHB resistance in a final field test planted in 2004.

Resistance tests

Trials were located at four sites: Hohenheim (HOH) near Stuttgart (geographic location: latitude 48.8°, longitude 9.2°; 400 m above sea level, 8.5°C mean annual temperature, 685 mm mean annual precipitation), Wohlde (WOH) near Celle (geographic location: latitude 52.8°, longitude 9.98°; 80 m above sea level, 8.8°C mean annual temperature, 753 mm mean annual precipitation), Wetze (WET) near Einbeck (geographic location: latitude 51.7°, longitude 9.0°; 130 m above sea level, 8.6°C mean annual temperature, 645 mm mean annual precipitation, and Seligenstadt (SEL) near Würzburg (geographic location: latitude 50.0°, longitude 8.9°; 281 m above sea level, 9.1°C mean annual temperature, 622 mm mean annual precipitation). All genotypes were planted in one row of 0.8 m length with 40 kernels per row. To avoid infection by other pathogens, all plots were sprayed once with Opus Top™ (BASF, Ludwigshafen, Germany) shortly before heading. The 113 marker-selected $F_{2:3}$ lines were tested in four replicates as complete randomized block design. Each of the four parents was included five times within each replicate.

Inoculum of two highly aggressive, DON-producing isolates of *Fusarium culmorum* (FC 33, FC 46) was produced on wheat grain medium as described in Miedaner et al. (1996). During flowering the spore suspension with a density of 5×10^5 spores per ml was applied at a rate of approximately 100 ml m^{-2} onto the heads with a machine-driven small-plot field sprayer (Hege 75, Waldenburg, Germany) in the evening to all experiments. To consider the variation in flowering date between entries, all genotypes including the parents were inoculated four times starting with onset of flowering. Inoculation dates were timed such that each genotype was inoculated at least once at its appropriate mid-flowering stage. Thus, all genotypes had the same weather conditions after each inoculation date. No mist irrigation was applied. To obtain a measure of disease progress, FHB rating was assessed on three successive dates beginning with the onset of symptom development, i.e. 14–22 days after inoculation depending on the environment in 3- to 4-day intervals. For each genotype, the percentage of infected spikelets was rated (0–100) on a plot basis. For data analysis, the arithmetic mean of all three ratings was used to improve accuracy. This is called mean FHB rating throughout the paper. Additionally, heading date was recorded on a time scale starting at 1st January and plant height as a mean height per row in centimeters.

Statistical analyses

All statistical analyses were based on plot means. All traits were analyzed separately for the locations and residual analyses were conducted for each trait to check normality of the data that was confirmed. Estimates of variance components were calculated as described by Snedecor and Cochran (1989) for factorial experiments. Analyses across locations were calculated using the means from the individual locations with the computer package PLABSTAT (Utz 2004). Multiple comparisons between means were performed using the residual maximum likelihood (REML) method within the PROC MIXED procedure of SAS/STAT (SAS Institute 2004). The effects of genotype and location were considered as random.

Results

A moderate infection level was achieved with mean FHB ratings ranging from 20.3 to 27.8% at the four locations. FHB resistance and plant height both had a high entry-mean heritability ($h^2 = 0.94$ and 0.99, respectively). Heading date was not associated with mean FHB rating as illustrated by the low, although significant, coefficient of correlation between both traits (-0.286, $P = 0.01$).

A lower FHB rating was found for all entries with donor-QTL allele(s). The effect of an individual QTL, however, was not significantly different from the marker class without any QTL (Table 2). Significant QTL effects on FHB rating were found only for the marker classes with two and three QTL combined amounting to 11% less FHB symptoms in the class with donor-QTL alleles 2BL + 6AL. However, the combination of donor-QTL alleles 2BL and 7BS was not significantly different from the classes with only one QTL, but its effect was still significant compared to the class without any donor-QTL allele. The four parents were significantly ($P = 0.05$) different in their susceptibility to FHB. None of the marker classes were, on average, as resistant than "Dream". All genotypes in marker classes with the donor-QTL allele on chromosome 6AL were on average 13.7 cm taller than the ones without this allele and hence even taller than the tallest of the parents. Nevertheless, significant ($P = 0.05$) variation for both traits was found among genotypes with donor-QTL allele 6AL (Fig. 1) and correlation between FHB rating and plant height was not significant ($P > 0.05$). A low number of shorter, fairly resistant lines with donor-QTL allele 6AL were detected.

Considerable genotypic ranges within the individual marker classes were found for FHB rating, only the class of genotypes having donor-QTL alleles on chromosomes 6AL + 7BS showed a smaller variation (Fig. 2). Even the distribution of genotypes having all three donor-QTL alleles overlapped with that of genotypes having no QTL alleles. Some of the lines in donor-QTL classes 2BL + 6AL + 7BS, 2BL + 6AL, and 2BL + 7BS were as resistant as the most resistant donor "Dream".

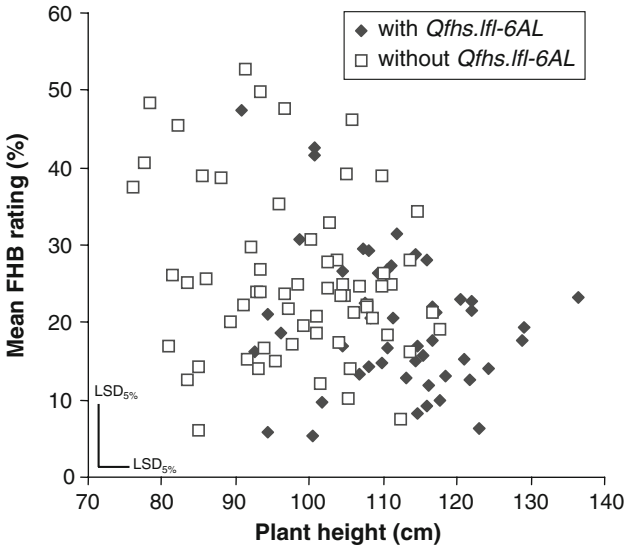

Fig. 1 Scatter plot distribution of pooled marker classes with and without the resistant allele of *Qfhs.lfl-6AL*, respectively, after inoculation with *Fusarium culmorum* across four locations in 2004. $LSD_{5\%}$ = least significant difference at $P = 0.05$

Comparing the effects for FHB rating with the original mapping populations showed that in our study all QTL effects were smaller (Fig. 3). Recovery was lowest for donor-QTL allele 7B, but considerably higher for the other two donor-QTL alleles. Donor-QTL alleles on chromosomes 6A and 7B still showed an additive effect. Averaged across the four classes, 64% of the effects from the mapping population could be recovered in this study.

Table 2 Means and effects of eight marker classes and parental means for *Fusarium* head blight (FHB) rating and plant height after inoculation with *Fusarium culmorum* across four locations in 2004

Entry	*N*	Mean FHB rating		Plant height	
		Mean[a] (%)	Effect[b] (%)	Mean[a] (cm)	Effect[b] (cm)
Marker classes:					
2BL + 6AL + 7BS	17	18.7 a	−10.6	107.7 ac	10.0
2BL + 6AL	9	18.0 a	−11.3	112.2 a	14.5
2BL + 7 BS	15	21.1 ab	−8.2	96.6 b	1.1
6AL + 7 BS	9	19.0 a	−10.4	116.4 a	18.7
2BL	9	22.4 bc	−6.9	101.0 c	3.3
6AL	14	23.7 bc	−5.6	112.9 a	15.2
7BS	18	26.6 bc	−2.7	99.3 b	1.6
None	22	29.3 c	–	97.7 b	–
Parents:					
Dream		6.4 A		104.8 A	
G16-92		15.6 B		107.1 A	
LP235-1		34.9 C		88.8 B	
Brando		55.5 D		79.1 C	

N number of lines

[a] Means followed by the same letter are not statistically different from each other at $P = 0.05$

[b] Difference to the class with no donor-QTL alleles

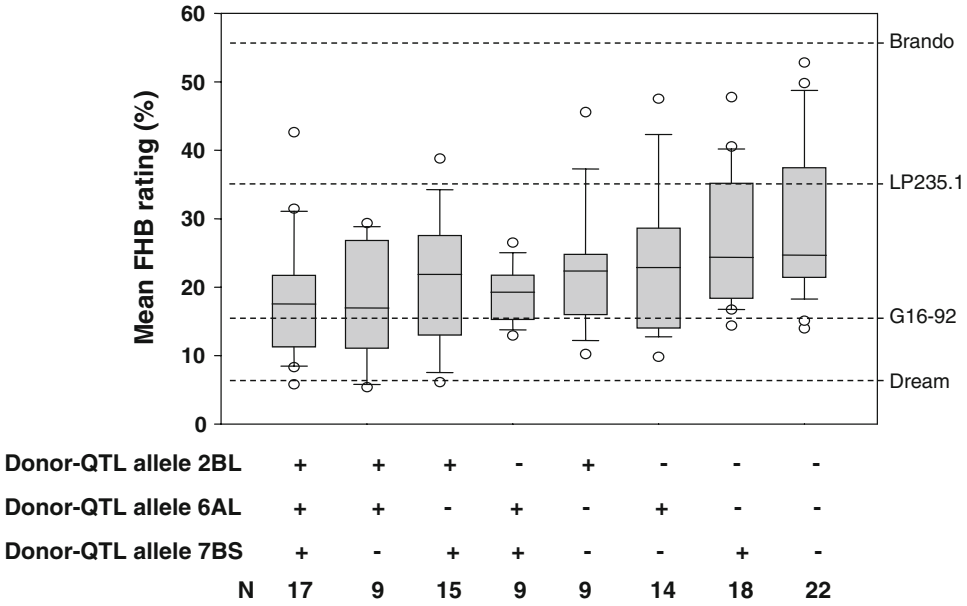

Fig. 2 Boxplot distributions of $F_{2:3}$ lines possessing alternative alleles (+, −: donor-QTL allele present or absent, respectively) at the FHB-associated QTL regions on chromosomes 2BL, 6AL, 7BS for FHB rating after inoculation with *Fusarium culmorum*. Data are based on mean values of the respective number (*N*) of lines across four locations. *Boxes* indicate the median (*solid line*), 25 and 75 percentiles, respectively, lines the 10 and 90 percentiles, respectively, and *dots* refer to outlying data points. Mean FHB rating of the parents of the double cross is indicated by *dotted lines*

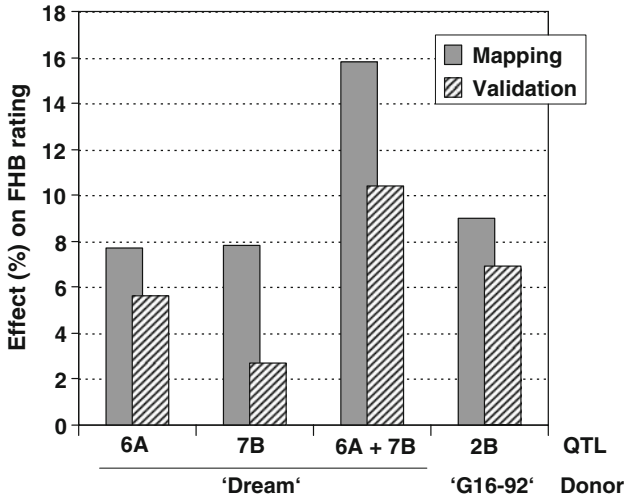

Fig. 3 Effect of the three donor-QTL alleles on chromosome 2B (from "G16-92"), 6A (*Qfhs.lfl-6AL*), and 7B (*Qfhs.lfl-7BS*, both from "Dream"), and the combination of the latter on *Fusarium* head blight rating (FHB) in the mapping populations and as reported in this validation study. "Effect" is defined as the effect of changing the allele at the respective QTL from susceptible to resistant. Both populations were tested across four locations, the mapping populations in 2002 by Schmolke (2005), our population in 2004

Discussion

Fusarium resistance is inherited quantitatively (Bai and Shaner 1994). Results of previous mapping studies indicate that FHB resistance in winter wheat is controlled by several QTLs with small to medium effects located in various regions of the wheat genome (Gervais et al. 2003; Klahr et al. 2004; Paillard et al. 2004; Schmolke et al. 2005, 2008; Semagn et al. 2007). We were the first to introduce three donor-QTL alleles from mapping populations of winter wheat in a different genetic elite background and to estimate their effects in different environments. This is necessary because breeders normally will not use the original mapping populations for further selection, but introduce the QTLs in their own elite material. It was our aim to demonstrate that mapping results can directly be used for practical plant breeding. FHB resistance provided by the QTLs studied reached significance also in the different background, however, only in combination of at least two donor-QTL alleles. The effects were smaller than in the original mapping population (Fig. 3). Accordingly, Utz et al. (2000) reported a reduction of about 50% between mapping and validation populations for quantitatively inherited agronomic traits. Recombination between marker and QTL might be one cause for this reduction. Only one SSR marker per QTL was available for this study and the markers had 2–8 cM distance between the QTL peak and the SSR marker used. The availability of markers is very restricted caused by low polymorphism for SSR markers in the mapping populations (22% for G16-92/Hussar and 30% for Dream/Lynx according to Schmolke 2005) and the need for diagnostic markers that can differentiate among the donor-QTL allele on one hand and the alleles of all other parents from the initial cross on the other hand (see Table 1). *Qfhs.lfl-7BS* had the lowest recovery effect, but also the largest distance to the used SSR marker (Haeberle et al. 2007). In contrast, for *Qfhs.lfl-6AL* distance was below 2 cM in a verification study and this QTL could be recovered rather efficiently (see Fig. 3). Another factor is a large bias of the precision of QTL mapping (Schön et al. 2004) that restricts testing accuracy especially when QTL effects are small (Melchinger et al. 1998).

The different genetic background of validation and mapping populations might be crucial. The two QTLs from the Dream/Lynx cross (*Qfhs.lfl-6AL, Qfhs.lfl-7BS*) were validated in a Dream/Lynx backcross population in the same magnitude than in the original mapping population (Haeberle et al. 2007). Instead, we used "Brando" and "LP235.1" as elite parents with unknown QTLs for FHB resistance. "LP235.1", however, was significantly ($P = 0.05$) more resistant than "Brando" (Table 2) and should, therefore, contain additional, yet undetected resistance-QTL alleles. In addition, lines in the marker class 6AL + 7BS with the two QTLs derived from "Dream" were, on average, more susceptible than the donor, because this variety has at least one additional QTL for FHB resistance on chromosome 2BL (Schmolke et al. 2005) that was not transferred. In three other marker classes, individual lines were similar resistant than "Dream" (see Fig. 2) illustrating the potential of marker-based selection when followed by phenotypic selection. The effects of the introduced QTLs originating from winter wheat were considerably smaller than those from the spring wheat source "CM82036" (*Fhb1, Qfhs.ifa-5A*) analyzed in a similar study and amounting to 17% reduction of FHB rating (Miedaner et al. 2006). This coincides with the fact, that also in the mapping populations the spring wheat-derived QTLs had higher effects (Buerstmayr et al. 2003 vs. Schmolke et al. 2005).

Both resistance donors in our cross were significantly taller than the elite lines with the mean difference of 22 cm across four locations (Table 2). One of the QTLs introduced, *Qfhs.lfl-6AL,* overlaps with a QTL for straw length within a 1.4 cM interval (Schmolke et al. 2005). In our study, progeny with this FHB-resistance QTL allele were also on average 13.3 cm taller and had fewer FHB symptoms (Table 2). The fact, that some marker classes are on average taller than the tallest of the parents illustrate that plant height is inherited by multiple loci leading to positive transgressions in the progeny. Despite this, some recombinants were already found among 113 progeny having the resistance-QTL allele and being fairly resistant and shorter (see Fig. 1).

In conclusion, the two introduced QTLs on chromosomes 2BL + 6AL were able to improve FHB resistance by about 40 percentage points compared to the marker class without any QTLs. The respective markers can, therefore, be used for rapidly introgressing additional QTLs into germplasm that is already medium resistant or in high-yielding, but susceptible material to fulfill the criteria for registration of cultivars. Marker selection for FHB resistance in winter wheat should, however, followed by phenotypic selection to achieve the most resistant progeny and efficiently use its advantages.

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